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LATITUDINAL DIFFERENTIATION IN EMBRYONIC DURATION, EGG SIZE, AND NEWBORN SURVIVAL IN A HARPACTICOID COPEPOD

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ABSTRACT

We demonstrate significant genetically based differentiation in embryonic duration (h), egg size (μm^3), and newborn survival (number/h) in the harpacticoid copepod, *Scottolana canadensis* (Crustacea), taken from a broad range of latitudes (°N) and reared in the laboratory for several generations under the same conditions. Egg development times of the northern-derived (ME) individuals were significantly longer at all test temperatures, and thus did not demonstrate compensation at low temperature. Maine development times may be due to the larger egg size.

INTRODUCTION

Compensatory responses to cold temperature are common in poikilotherms (Bullock, 1955, 1957). Compensation is manifested in cold-adapted animals by an elevated physiological rate compared to those that are warm-adapted (yet see Barlow, 1961; Pickens, 1965). Adaptation to low temperature, involving metabolic acceleration, results in substantially increased energetic costs at high temperatures, which may result in little energy available for growth or reproduction (Levinton, 1983). This may lead to stabilizing selection for latitudinally fixed physiological rates and thus geographic variation in gene frequencies, or local evolution.

In marine invertebrate traits such as metabolic rate, thermal limits, and egg development, reversible and irreversible environmental effects may both be responsible for latitudinal (Schneider, 1967) or seasonal variation whereas genetic effects may be very minor (Vernberg, 1972; Landry, 1975). In contrast, other studies have suggested that phenotypic differences may reflect local genetic adaptation (Gonzalez, 1974; Bradley, 1975, 1978; Levinton and Monahan, 1983; Lonsdale and Levinton, in press). The sources of physiological and morphological differences between and within populations can be estimated from progeny reared in the laboratory under uniform environmental conditions. This method eliminates both the reversible and irreversible components of physiological adaptation. If a difference is then found among progeny reared under identical laboratory conditions it would suggest that the difference is genetical (Battaglia, 1957; Schneider, 1967; Antonovics *et al.*, 1971).

In this paper we present data that demonstrates genetically based differences in embryonic duration and egg size among latitudinally separated individuals of *Scottolana canadensis* (Willey), a harpacticoid copepod. Our results do not demonstrate compensation for temperature in egg development but we suggest that it may be masked by differentiation in egg size.

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Materials and Methods

Field collections

Scottolana canadensis is a brackish-water species (Coull, 1972), whose peak population growth is restricted mainly to late winter through early summer along the Atlantic coast (Willey, 1923; Lonsdale, 1981a; B. Coull, pers. comm.). Planktonic nauplii and epibenthic adults were obtained at five sites on the east coast of North America; pertinent collection information is listed in Table I. Separate collections consisted of 250 or more nauplii and a few adults except those for FL-1981 which consisted of 30–40 nauplii. Approximately 50–75% survived transport and reached reproductive age. All five collections appear to contain *S. canadensis* on the basis of morphology (B. Coull, pers. comm.) and reproductive compatibility, although the latter diminishes with distance between the locales (Lonsdale and Levinton, unpubl.).

Culture methods

In the laboratory, wild-caught copepods were cultured through one generation in 1000- and 2000-ml Erlenmeyer flasks containing Millipore-filtered (0.45 μm) ambient estuarine water. Subsequently, water obtained from Stony Brook Harbor, New York, was used for culture after being glass-fiber filtered, adjusted to 15‰ with distilled water, and autoclaved. Algae were cultured at 20°C and 15‰ with a 14:10 hour light-dark cycle in f/2 nutrient medium (Guillard, 1975) and maintained in approximately a log phase of growth by harvesting and media addition five times weekly. Algae cultures used both in copepod culturing and experiments ranged in age from 5 to 14 days. Assessments of cell densities were made using a hemocytometer or Coulter counter.

A mixture of three algal species, *Isochrysis galbana* (ISO), *Pseudoisochrysis* sp. (VA12), and *Thalassiosira pseudonana* (3H), was added to each copepod culture flask four times weekly in 1981 and 1982; twice to obtain a minimum density of 1.0×10^5 cells/ml and alternatively to achieve 2.5×10^5 cells/ml. Previous experience

Table I

Location and physical characteristics of collection sites for Scottolana canadensis

Collection site	Latitude (°N)	Date	Temperature (°C)	Salinity (‰)
Tampa, FL	27	May 1981	27	18
		April 1982	24	18
		March 1983	19	18
Georgetown, SC	33	May 1981	24	15
Lusby, MD	38	May 1981	24	10
		May 1982	20	10
		May 1983	20	10
Mattapoisett, MA	41	June 1981	21	10
		June 1983	23	10
Biddeford, ME	43	June 1981	15	15
		May 1982	13	10
		July 1983	19	10

had shown that high rates of copepod mortality occurred when *Scottolana* were fed greater rations. Presumably, this was from the detrimental effects of substantial settling of algal cells. In 1983, the feeding routine was altered so that each culture reached a minimum density of 2.5×10^5 cells/ml three times weekly.

Harvesting of the copepod cultures was begun when wild-caught females began to reproduce. The vast majority of nauplii (nauplius stages I–VI) were found in the upper water column and adults occurred on the bottom of the culture flask. In 1981 and 1982, nauplii were removed weekly by pouring off 25–30% of the culture water. Once a month adult densities were substantially reduced; 50–75% of the adults were removed but a major proportion of nauplii, those that passed through a sieve or were collected with the surviving adults, were retained. Retained nauplii, in addition to subsequently hatched nauplii, were not harvested until the second week following this procedure. At this time, 50% of the copepod culture water was replaced. Initially, some harvested adults were used to start replicate cultures or ones at other temperatures differing from ambient (15, 20, 25, or 28°C). This procedure allows an approximate calculation of the number of generations since a population was removed from the field. All cultures at a given temperature received equal feeding and harvesting treatments with the exception of the FL-1981 culture; nauplii of the first generation (f1) were not harvested and those from the second generation (f2) were used to start other cultures.

Because of coinciding experiments in 1983 that required the frequent (at least once a month) removal of a majority of gravid females in all cultures, it was not necessary to routinely split them as was done in previous years.

Experimental procedures

Egg development times. One hundred and fifty to two hundred f2 nauplii (1981) were removed from each representative culture (n = 15) and reared in 1000-ml beakers containing autoclaved, glass fiber-filtered sea water (15‰). They were fed an algal suspension of *I. galbana* and *T. pseudonana* in equal cell densities and adjusted to 2.5×10^5 cells/ml four times weekly. From these cultures 50 mating pairs were removed and maintained under these same conditions until females began producing eggs. To determine egg hatching times, females were then placed individually in separate wells (1-ml volume) of a multi-depression dish placed in an airtight opaque plastic box. Distilled water in the bottom of the box reduced evaporation from the wells. The culture media, as above, was replaced daily. The location of boxes within an incubator was randomized with respect to locality. Females were monitored every four hours for the appearance of an egg sac and until the time of egg hatching. Approximately ten observations were made at 15 and 20°C while 20 were made at 25 and 28°C. Only three observations were made at both 25 and 28°C for the FL-1981 samples because females had little reproductive success. Also, FL-1981 hatching times were not determined at 15 and 20°C nor were SC-1981 at 15°C because these cultures were not established at the time.

The procedures were repeated for all populations in 1983, (excluding SC) using nauplii from cultures that had been in the laboratory for four to six months. Since in most cases there were not 50 mating pairs, the second step was eliminated; reproductive females for experimental monitoring were removed from the initial experimental culture and placed directly in the depression plates. Sufficient numbers of FL-1983 females reproduced during this series of experiments except at 15°C.

Egg size. To test for among-locale differences in copepod egg size, experiments were conducted in 1982 and 1983; the first was a preliminary study at 20°C, and

the second involved a range of temperatures (15–28°C). In the preliminary experiment, 150 to 200 f2 nauplii from three locales (ME-, MD-, and FL-1982) were removed from 20°C cultures and reared under the same conditions as nauplii used in the egg development studies. When females produced egg sacs, they were isolated in 50-ml Stendor dishes containing 20 ml of the same media and observed daily for newly hatched nauplii. Approximately 15 to 20 f3 nauplii from 10 females were removed and again reared in the same manner as the previous generation. Once mating was observed, the beakers were checked daily for the presence of egg sacs on females which were then removed and preserved in 5% buffered formalin. A time-limitation is necessary in order to minimize egg size increases from water uptake (Wittman, 1981). In the second series of experiments, females used in the above described 1983 egg development experiments also were preserved within 24 hours of extruding a second clutch of eggs.

The egg sacs were dissected and, when possible, egg dimensions (μm) were determined for four to six eggs for each of 10 females from each locale and test condition. Egg volume was calculated after Allan (1984) by the formula: volume (μm^3) = $4/3\pi r_1 r_2^2$ where r_1 and r_2 are the long and short axis, respectively.

Newborn survivorship. One hundred and fifty to two hundred f4 nauplii from each 1981 locale (ME, MA, MD, SC, FL) were reared at 25°C using the same procedure as that for f2 nauplii used in the egg development studies. From these cultures gravid females were isolated and observed every 12 (±2) hours until the eggs hatched. The nauplii were individually placed in separate wells of a multi-depression dish as already described. From each of six families, six siblings were equally split among two food levels, 2.5×10^4 and 5.0×10^5 cells/ml; n = 18 for each locale and ration. Media in the wells was completely replaced daily for nauplii and copepodites. When Copepodite I was reached, an additional 50% was replaced 12 hours later. The location of individuals in an incubator was randomized with respect to family, locale, and food density. Observations on stage of development (6 nauplius, 5 copepodite, and the last adult molt stage) and mortality were made every 12 (±2) hours.

Results

Egg development times

Differences in embryonic duration (h) were not found within localities between years (1981 and 1983) for FL, MD, and MA eggs. (A Two-way ANOVA for year and temperature effects was computed for each locale.) But in 1983, ME eggs on the average took 10% longer to develop ($P < 0.001$) at each temperature than they had in 1981. As there was no temperature-year interaction, we pooled development data for both years for ME as well as for the remaining locales. For all locales, including SC-1981 (One-way ANOVA), temperature was a highly significant factor ($P < 0.0001$). The relationship between development time and temperature was best described by a linear regression for both ME and MA populations ($r^2 = 0.83$ and 0.85; Fig. 1) and a log-log regression for MD, FL, and SC ($r^2 = 0.86$, 0.90, and 0.71, respectively. For SC, the log-log regression was only marginally better, since r^2 increased by less than 1%, because of the absence of 15°C data). We used a Two-way ANOVA for locale (excluding SC because of the absence of 15°C data) and temperature effects (15–25°C) to explore the possibility of genetically based latitudinal differentiation in egg development rate. Both variables and their interaction term were highly significant ($P < 0.0001$). This analysis indicates both genetic differentiation of copepods among locales and a locale by temperature source of variance.

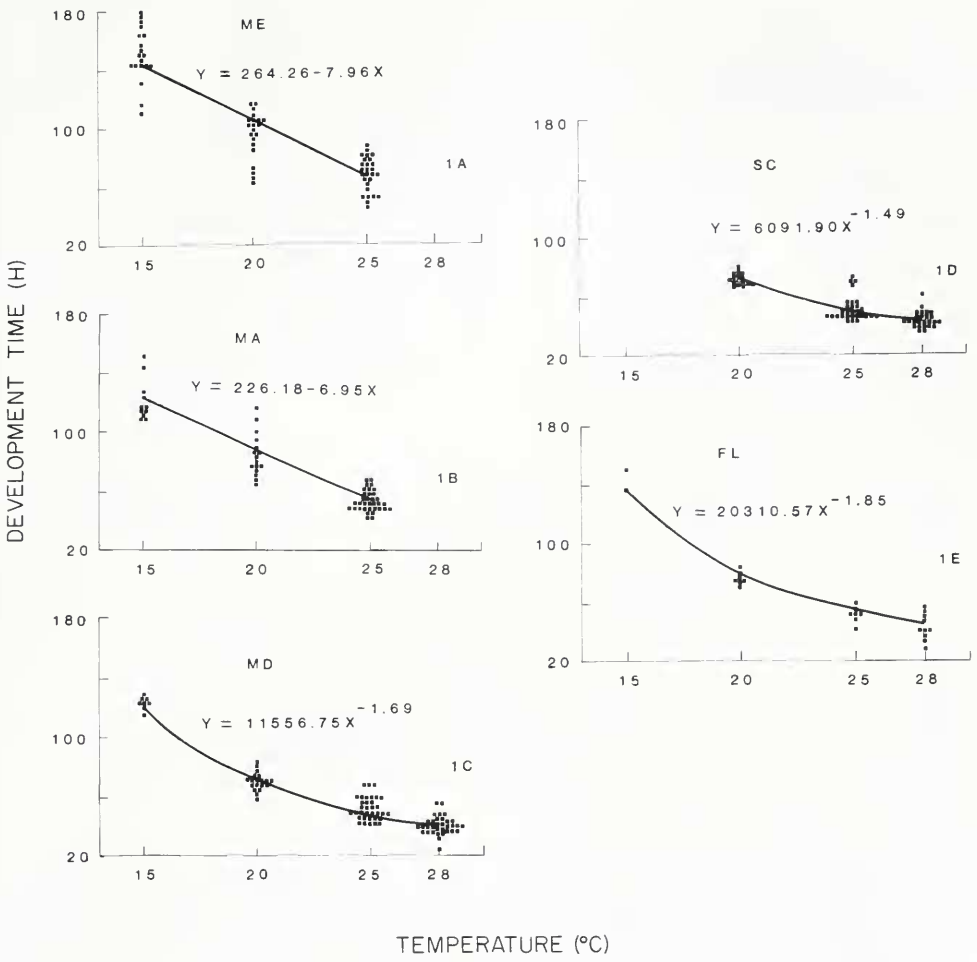

FIGURE 1. Egg development times (h) of *Scottolana canadensis* collected from five locales (ME, MA, MD, SC, FL) and tested at four temperatures (15, 20, 25, 28°C).

Differences in egg development time (h) between some locales were found at each temperature despite culturing under identical conditions (Table II; One-way ANOVA followed by a Studentized Range test; Snedecor and Cochran, 1967). Most striking was the slower egg development rate of the ME copepods at all temperatures tested (15, 20, and 25°C. We were not able to establish ME or MA cultures at 28°C). In contrast, MD, SC, and FL times are similar between 20 and 28°C. At 15°C, the mean hatching time of FL eggs is significantly greater than MD and SC, but because of the small sample size, n = 2, we are not confident in this result.

From these data, acceleration of egg development, as found for growth (Lonsdale and Levinton, in press), at low temperature is not readily apparent in high-latitude *Scottolana.*

Egg size

In the preliminary 1982 egg size study conducted on f3 females at 20°C, significant differences were found among the three test locales (ME, MD, FL), as

TABLE II

Mean egg development times (h) of Scottolana canadensis *collected from five locales and reared at four temperatures (°C)*

Locale	Temperature (°C)			
	15	20	25	28
ME	149.2[a]	97.3[a]	67.7[a]	—
MA	123.1[b]	85.8[b]	52.7[b]	—
MD	122.5[b]	70.4[c]	52.4[b]	40.7[a]
SC	—	71.9[c]	51.0[b]	43.9[a]
FL	143.6[a]	76.7[b,c]	51.7[b]	44.1[a]

Means with identical superscripts (a, b, or c) are not significantly different (.05 level) at a given temperature.

well as among females within a locale ($P < 0.005$; Nested ANOVA). Eggs of ME females were the largest, averaging $1.56 \pm .12 \times 10^5$ μm^3 (±95% confidence), MD were intermediate, $1.27 \pm .04 \times 10^5$ μm^3, and FL were the smallest, $1.07 \pm .07 \times 10^5$ μm^3.

In 1983, both the latitude from which the copepod originated and the rearing temperature were significant variables affecting the mean egg volume of a female *Scottolana* ($P < 0.001$ and $P < 0.0002$, respectively; multiple regression). As in the previous year, egg volumes of ME females were the largest, whereas there was no difference between MD and FL eggs (Fig. 2). The influence of temperature is only apparent between 15 and 20°C; egg volumes are substantially reduced at 20°C in all populations. There is no further reduction in volume between 20 and 28°C.

Newborn survivorship

Newborn survivorship curves constructed from the copepod growth rate experiment conducted at 25°C and 2.5×10^4 cells/ml are shown in Figure 3. At this ration, survivorship was poor for all five populations. At the termination of the

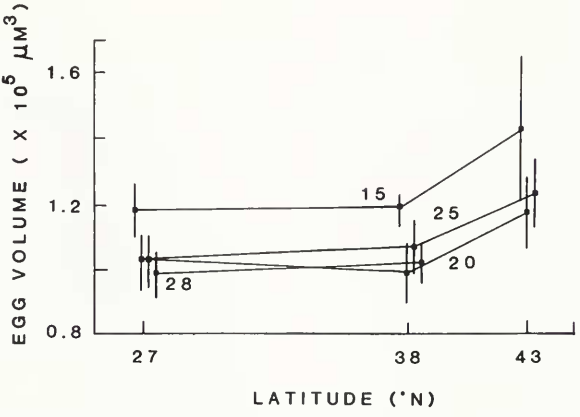

FIGURE 2. Mean egg volumes ($\times 10^5$ μm^3; ±95% confidence) of *Scottolana canadensis* collected from three locales (ME, MD, FL) and tested at four temperatures (15, 20, 25, 28°C).

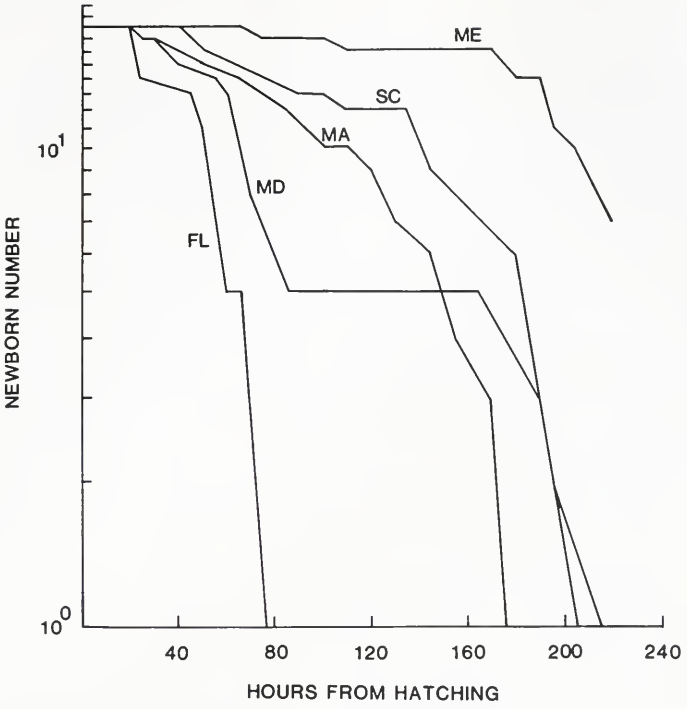

FIGURE 3. Newborn survival (number/h) of *Scottolana canadensis* collected from five locales (ME, MA, MD, SC, FL) and reared at 25°C and 2.5×10^4 cells/ml.

experiment, 220 hours, no nauplii had reached Copepodite I, (ME nauplii had developed the fastest, reaching Naupilus V), and most nauplii were dead. Insufficient food levels were the cause of these results since sibs maintained at 25°C and 5.0×10^5 cells/ml grew faster, many copepods had reached adult by 200 hours, and had substantially higher rates of survival. After 120 hours at the high ration, all newborns had survivorship rates of 94% or better and at 220 hours, all were greater than 70%; MD nauplii had the lowest rate of survival, 75%, followed by ME, FL, MA, and SC (78, 83, 94, and 100%, respectively). There is no latitudinal differentiation in survivorship at the high ration ($P > 0.145$; Gehan-Wilcoxin test; SAS). In contrast, at the reduced ration, significant differences among survivorship curves emerge ($P < 0.0001$). Maine nauplii had a higher survivorship rate compared to all other populations; 36% were alive after 220 hours whereas 100% mortality of FL nauplii occurred by 120 hours. Massachusetts, MD, and SC survivorship curves were similar among one another, and intermediate between those from ME and FL.

DISCUSSION

We show genetically based variation in three reproductive traits of latitudinally separated *Scottolana canadensis;* embryonic duration (h), egg size (μm^3), and newborn survival (number/h). High-latitude copepods from ME produce eggs that take longer to develop and that are the largest when compared to all other east

coast copepods. Their nauplii also have the highest rates of survival when food is limiting.

Our data do not demonstrate acceleration in embryonic development for animals from low-temperature locales. Rather, the opposite is true because high-latitude eggs take a significantly longer time to develop. These results are in direct contrast to those reported for inter- and intraspecific embryonic development times in cold- and warm-adapted rotifers and copepods (Herzig, 1983a, b; yet see Hart and McLaren, 1978). Although there are many biological factors that can influence embryonic duration, such as DNA content of the dividing cells or cytoplasmic clocks (Horner and MacGregor, 1983; Hara *et al.*, 1980; respectively), we feel that the latitudinal differentiation in egg development times demonstrated in our study is a consequence of variation in egg size. Maine females produce the largest eggs, which in turn have the longest development times. It has often been observed that larger eggs have longer development times (McLaren, 1966; Corkett, 1972; Bottrell *et al.*, 1976; Steele, 1977; Hart and McLaren, 1978; Woodward and White, 1981; Clarke, 1982.). Several phenomena could explain this correlation but a common explanation is that the rate of carbon dioxide or oxygen diffusion in large eggs may be slower when compared to that for smaller eggs (Berrill, 1935; cited by McLaren, 1966; Clarke, 1982). Diffusion rates would then necessitate a lower metabolic rate (Corkett, 1972). This fact may explain why egg survival is most drastically reduced in species with large eggs when temperatures are elevated (Wear, 1974); diffusion rates may not be sufficient to meet the increased metabolic requirements.

The question then arises as to why ME females produce larger eggs. A positive correlation between egg size and body size is known in some copepods (Hart and McLaren, 1978). Thus ME females may produce eggs that are larger because of their larger body size at all test temperatures compared to FL females (Lonsdale and Levinton, in press). But body size alone cannot explain egg size differences between ME and MD females because their body lengths are similar. Variation in egg yolk content also can contribute to egg size differences. Our hypothesis is that ME *Scottolana* females produce eggs that contain more yolk than those from other locales (MA, MD, SC, and FL), resulting in eggs which are larger and which take longer to develop. At least four possible processes, listed below, may be operating to explain this pattern.

(1) Differential dietary requirements among *Scottolana* populations; experimental algal diets may not be equal in nutritional value and insufficient maternal diets can reduce energy reserves in eggs.

(2) Energy budget limitations imposed by local temperature conditions; higher environmental temperatures, as in FL, may result in less energy available for reproduction thereby resulting in females producing both fewer as well as less costly eggs.

(3) Variability in primary productivity during the nauplius planktonic stage; restrictions in the more northerly latitudes may necessitate some degree of independence from environmental food resources.

(4) Limited nauplius development time imposed by cold coastal temperatures; yolkier eggs may shorten the planktonic phase and thereby decrease the probability of *Scottolana* being carried into the Gulf of Maine.

Differential dietary requirements

The diet used in both the egg development and egg size experiments has been shown to maximize growth and reproduction in MD *Scottolana* (Harris, 1977) but

it is equally good for ME, MA, and SC copepods. For example, in this study, the diet resulted in 88, 79, 75, and 87% successful hatching rates of clutches at 20°C for the four populations, respectively. We also have data (unpubl.) which show that the numbers of eggs produced by MD and ME females, corrected for body weight, are not significantly different at any test temperature (15–25°C) and greater than 80% of all adult females produce clutches when food is not limiting. (We did not test either MA or SC females for egg production.) It is apparent from these data that food inequities in the laboratory cannot explain the substantial differentiation in embryonic duration, egg size, and newborn survival, which are presumed to result from greater egg yolk reserves of the ME population relative to the remaining three (MA, MD, and SC) east coast *Scottolana* populations.

In contrast, FL females may have different dietary requirements. Florida females also are very fecund at all test temperatures (15–25°C), since greater than 80% of all adult females reproduce (Levinton and Lonsdale, unpubl.), but in this study at 20°C only 38% of the clutches produced resulted in viable nauplii. The experimental diet may be inferior if assimilation efficiencies are reduced in FL females but our data (unpubl.) show no significant difference in carbon assimilation efficiencies between ME and FL females feeding on *I. galbana* at 20°C. Diet also can affect reproduction if specific vitamin or sterol (lipid) requirements are not met. In many insects, particularly *Drosophila,* proteinaceous materials are necessary for yolk formation, whereas the metabolic pathways associated with this process depend on vitamin, sterol, and salt availability (Engelmann, 1970). Cholesterol has been shown not to affect the number of eggs laid by *Drosophila,* but its deficiency results in low hatching success (Sang and King, 1961; cited by Engelmann, 1970). Egg hatching success in our laboratory-reared FL populations has been inferior to all other populations throughout our three years of study. This does not necessarily mean that yolk content is reduced in the FL eggs, however. First, inviability could be due to male sterility from vitamin deficiencies (Geer, 1966; cited in Engelmann, 1970). But male sterility is most likely not important since our breeding experiments (unpubl.) have shown that FL females are no more fertile with males from other populations despite the fact that other populations have successful hatches more than 80% of the time. Second, if egg maturation is controlled by hormones, nutritional deficiencies may alter only the endocrine system and not yolk formation (Engelmann, 1970).

Energy budget limitations

At higher temperatures, proportionately less energy may be available for reproduction (Sebens, 1982; Barber and Blake, 1983; Page, 1983; yet see Glebe and Leggett, 1981). Increased temperatures may impose additional metabolic demands not met by increased feeding rates (Sebens, 1982; Levinton, 1983). Thus, reproductive energy constraints, mediated by the local thermal regime, may select for egg size and/or its yolk content in addition to egg number. But lecithotrophic reproduction does not necessarily require greater reproductive effort. In some cases related species show no significant difference in reproductive effort between reproductive modes and in others, planktotrophic effort may exceed that of lecithotrophic effort (DeFreese and Clark, 1983; Todd, 1979; respectively. In both papers, "effort" is defined as egg mass calories per adult calorie.) Given that higher temperatures can restrict the amount of energy available for reproduction, these findings show that it does not necessarily follow that individual eggs will have less allocated energy and thus temperature is not the ultimate factor operating to explain the patterns of differentiation found in this study among latitudinally separated *Scottolana.*

Variability in primary productivity

Variability in primary productivity among locales also may explain our results. Thorson (1950) noted that Arctic marine benthic invertebrates produce large, yolky eggs whose larvae are without a planktonic phase while most temperate species produce eggs with very little yolk and subsequently, the larvae are planktotrophic. Although energetically expensive, yolky eggs have presumably evolved because primary productivity is seasonally restricted in high latitudes and developmental periods are longer, making successful planktotrophic feeding unpredictable if not impossible for many species. Todd (1979), studying two sympatric species of nudibranchs, also has suggested that lecithotrophy may have evolved "in order to offset the unpredictability of energy available for reproduction" (p. 57). In the laboratory, the reproductive strategy of *S. canadensis* is characterized by a long reproductive lifespan (>60 days at 20°C; Lonsdale, 1981b) and in the field gravid females have been found in late summer although planktonic nauplii are rare (Lonsdale, 1981a). Thus, ME nauplii from the first few clutches may complete development within the spring bloom period, but the later ones must contend with declining concentration and changing composition of algae as well as possible increased competition from other dominant copepods such as *Acartia* (Townsend, 1984; B. McAlice, pers. commun.; Lonsdale, pers. obs.).

The variable primary productivity hypothesis is supported by our data which show a correspondance between *Scottolana* embryonic development time, egg size, and the ability to survive as nauplii when food is severely limiting. Planktonic feeding must be a necessity for FL Nauplius II–III as they did not survive past these stages when reared at 25°C and 2.5×10^4 cells/ml. In contrast, 36% of ME nauplii had reached Nauplius V at the termination of the experiment (220 h). Excess nutrient reserves sequestered in the cells or gut of newly hatched ME nauplii could explain these very different rates of survival. Other studies also have shown that egg size and larval survival are directly correlated in marine bivalves and yolk content is presumed to determine this relationship (Bayne *et al.*, 1975; Kraeuter *et al.*, 1982). It also is possible that the increased rates of survival in high-latitude forms under low food stress could result if their nauplii were more efficient filter-feeders but had metabolic costs which were similar to low-latitude nauplii. This alternative is not as reasonable given the larger body size of ME nauplii (Lonsdale and Levinton, unpubl.) and the observation that the optimal body size for maximum scope for growth decreases as food supply declines (Elliott, 1975; Vidal, 1980; Sebens, 1982).

Nauplius development time restrictions

The Saco River, from which the ME *Scottolana* were collected, is characterized by extremely heavy freshwater flow as compared to other estuaries along the Maine coast (B. McAlice, pers. comm.) and it is highly likely that nauplii would be lost once carried into the Gulf of Maine due to rapidly declining temperatures (McAlice, 1981). Yolkier eggs may enhance the rate of nauplius development to Copepodite I, at which stage they migrate to the bottom, thereby increasing the probability of *Scottolana* remaining within the estuary. Our data reported in this paper indicate that when food is extremely limiting, (2.5×10^4 cells/ml), ME nauplii have the developmental advantage at 25°C. We also have data (unpubl.) which show a similar result at a less restrictive ration and lower temperature. We have found that at 15°C there is no significant ration effect (5.0 *versus* 1.0×10^5 cells/ml; $P > 0.05$; One-way ANOVA) on total time from hatching to Copepodite I for either FL or

ME nauplii. However, at 20°C, the time is significantly increased at the lower ration for nauplii from FL but not from ME. At 25°C, the development time of nauplii from both locales is significantly affected but ME less so than FL (82 *versus* 98 h at 5.0 and 1.0×10^5 cells/ml, respectively, for ME nauplii as compared to 85 *versus* 126 h for FL). Although ME nauplii are not at a developmental advantage at the high ration, since there were no significant between-locale differences at 15, 20, or 25°C ($P > 0.05$; One-Way ANOVAs), we cannot rule out the possibility that ME females produce yolkier eggs which enhance nauplius development rates in order to minimize loss of offspring from the estuary. It is difficult to assess how well our laboratory food levels match that which copepods experience in estuaries.

We feel that either variability in planktonic productivity and/or nauplius developmental time restrictions may be operating to explain the patterns of differentiation in embryonic duration, egg size, and newborn survival among latitudinally separated *Scottolana canadensis*. All three traits can be affected by egg yolk content, and it is this latter trait which is being selected upon in response to environmental factors. Further inquiries into the extent of differentiation in egg yolk content among *Scottolana* populations is warranted.

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